

Analysis of harvest strategies for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska

J. Zheng, M.C. Murphy, and G.H. Kruse

Abstract: A modifiable harvest rate constrained by a minimum spawning abundance (threshold) is currently used to set the annual harvest level for Bristol Bay red king crab, *Paralithodes camtschaticus*. A length-based simulation model was constructed to evaluate effects of recruitment, natural mortality, and handling mortality on this harvest strategy. Evaluation criteria included mean yield, stability of yield, harvest opportunity, and stability of spawning stock. Optimal mature male harvest rates were strongly negatively related to handling mortality. For any given harvest rate, handling mortality is a key factor influencing optimal thresholds. The current harvest strategy produces a high mean yield and low variability in yield under low handling mortality scenarios, but the population is at high risk of collapse with a high handling mortality. Given uncertainties of recruitment, natural mortality, and handling mortality estimates, we recommend reducing mature male harvest rate from 20 to 15% and maximum legal male harvest rate cap from 60 to 50%. If handling mortality rate is greater than 30%, then we recommend increasing the threshold from 6600 to 11 000 metric tons of effective spawning biomass. Our recommended harvest strategy produces a mean yield similar to the current harvest strategy and safeguards against recruitment overfishing.

Résumé : Un taux de récolte modifiable lié à une abondance de frai minimale (seuil) est actuellement utilisé pour établir le niveau de récolte annuel du crabe royal, *Paralithodes camtschaticus*, de la baie Bristol. Un modèle de simulation fondé sur la longueur a été élaboré pour évaluer les effets du recrutement, de la mortalité naturelle et de la mortalité liée à la manipulation sur cette stratégie de récolte. Les critères d'évaluation comprennent le rendement moyen, la stabilité du rendement, les occasions de récolte et la stabilité du stock de reproducteurs. Les taux de récolte optimaux des mâles à maturité présentaient une corrélation fortement négative avec la mortalité liée à la manipulation. Quel que soit le taux de récolte, la mortalité liée à la manipulation est un facteur clé influant sur les seuils optimaux. La stratégie de récolte actuelle entraîne un rendement moyen élevé et une faible variation du rendement dans des scénarios de faible mortalité liée à la manipulation, mais la population est fortement exposée à un effondrement si la mortalité liée à la manipulation est élevée. Étant donné les incertitudes touchant les estimations du recrutement, de la mortalité naturelle et de la mortalité liée à la manipulation, nous recommandons une réduction du taux de récolte des mâles à maturité de 20 à 15 % et un plafonnement du taux de récolte des mâles de taille légale de 60 à 50 %. Si la mortalité liée à la manipulation est supérieure à 30 %, nous recommandons alors d'augmenter le seuil de 6 600 à 11 000 tonnes métrique de biomasse de frai réelle. La stratégie de récolte que nous recommandons entraîne un rendement moyen semblable à celui de la stratégie de récolte actuelle et assure une protection contre la surpêche affectant le recrutement.

[Traduit par la Rédaction]

Introduction

Harvests of red king crab (RKC), *Paralithodes camtschaticus*, in Bristol Bay, Alaska, have been characterized by dramatic fluctuations in abundance. The fishery began in 1930 and was conducted primarily by the Japanese and Russians before 1971 (Otto 1986). During the late 1960s, the U.S. fishing fleet gradually expanded, and by 1974, all foreign fishing for RKC was phased out. The domestic fishery peaked in 1980 with a yield of 59 000 t (metric tons). The stock crashed and no fishing was allowed in 1983. Since 1984, yield and stock abundance

have stayed at low levels (Griffin and Ward 1994; Stevens et al. 1994).

The Bristol Bay RKC fishery is cooperatively managed by the State of Alaska and the U.S. federal government. Two major management objectives for the fishery are to maintain a healthy stock that ensures reproductive viability and to provide for sustained levels of harvest over the long term that avoid fishery-induced boom-and-bust cycles (ADF&G 1994). In attempting to meet these objectives, management practices continue historical size–sex–season (3S) policies, i.e., harvest of males only ≥ 135 mm carapace length (CL) and no fishing during spring molting and mating periods (ADF&G 1994). In addition, fishing effort is controlled through vessel registration, pot limits, and other gear restrictions (ADF&G 1994). Catch is based on a modifiable harvest rate strategy constrained by a minimum spawning abundance. Under the current management plan, a 20% mature male harvest rate is applied to the abundance of mature (≥ 120 mm CL) males with a maximum 60% harvest rate cap of legal (≥ 135 mm CL) males (Pengilly and Schmidt 1995). The stock has been

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assessed each year since 1968 by the National Marine Fisheries Service (NMFS) with a trawl survey conducted from May to August (Stevens et al. 1994). Recently, a length-based model was developed to improve abundance estimates (Zheng et al. 1995a).

The current mature male harvest rate and maximum legal male harvest rate for the Bristol Bay RKC fishery are based on results of a simulation study for the Kodiak RKC fishery (Schmidt and Pengilly 1990). Comprehensive computer simulation studies on optimal harvest strategies were conducted for the Bristol Bay RKC fishery by Balsiger (1974) and Reeves and Marasco (1980). Balsiger (1974) estimated the maximum equilibrium yield to be 11 400 t, which is less than the mean observed yield during the last three decades. Reeves and Marasco (1980) apparently overestimated productivity of Bristol Bay RKC and suggested an optimal yield of 50 000 t. In addition to lack of adequate information to estimate stock-recruitment (S-R) relationships and natural mortality, all previous simulation studies used deterministic models that could not be used to examine the risk of population collapse.

A threshold was added to existing management measures in 1990 to avert recruitment overfishing (Pengilly and Schmidt 1995). The threshold is defined as the minimum mature female abundance "that allows sufficient recruitment so that the stock can eventually reach a level that produces MSY (Maximum Sustained Yield)" (NPFMC 1989). If population size falls below the threshold value, no fishing is allowed.

A threshold of 8.4 million fertilized females was estimated for Bristol Bay RKC by applying Thompson's rule (Thompson 1993) of 20% equilibrium spawning stock to the Ricker S-R model (NPFMC 1990). In practice, 8.4 million mature (≥ 90 mm CL) females have been used as the threshold level (Pengilly and Schmidt 1995). Application of this estimation method may not be appropriate because (i) Thompson's rule was derived from strong depensatory S-R models whereas this crab stock was fit with traditional Ricker curves (NPFMC 1990) or weak depensatory S-R curves (Zheng et al. 1995a) that do not need thresholds according to Thompson's findings and (ii) this approach does not account for handling mortality of female and sublegal crab, which could be substantial and vary from year to year.

In recognition of these problems, we used an alternative method to define and estimate an optimal threshold level. We defined threshold differently as a percentage of pristine effective spawning biomass, SP_{∞} . Following Zheng et al. (1995a), effective spawning biomass was calculated from estimates of male reproductive potential and spawning female abundance. Male reproductive potential is the sum of mature male abundances by CL, each multiplied by the estimated maximum number of females with which a male of that particular CL can mate (Zheng et al. 1995a). The number of females induced to ovulate and the percentage of eggs fertilized depend on male body size (Paul and Paul 1990). Large mature males are able to mate multiple females during a mating season (Table 1).

Although the threshold concept has been applied to RKC fisheries in Bristol Bay and elsewhere in Alaska, a thorough evaluation of Alaskan threshold criteria and harvest levels has not been performed. The purpose of this study was to analyze harvest strategies for Bristol Bay RKC with different threshold levels and harvest rates under variable environmental conditions, several handling mortality rates, and different weights

applied to different management objectives. We simulated RKC population dynamics by adding stochastic environmental effects to a length-based population model and an S-R model developed and updated by Zheng et al. (1995a, 1995b, respectively). A harvest model was used to simulate population and fishery outcomes from alternative parameterizations of three components of harvest strategy: threshold, mature male harvest rate, and maximum legal male harvest rate. We analyzed optimal levels of each component individually and in combination with each other in response to environmental variability, handling mortality rate, and management objective. Based on our findings, we formulated a new harvest strategy that is robust to these factors. We then conducted a sensitivity analysis of our robust strategy to structural errors in shape of the S-R curve, decadal-scale changes in natural mortality, and handling mortality rates.

Methods

Population parameters

The length-based population model used here is identical with that developed by Zheng et al. (1995b) and is summarized in the Appendix. Population parameters were obtained from Zheng et al. (1995b) and are summarized in Table 1. For convenience, all size measurements in this study are CL in millimetres. Population abundances were simulated annually during June each year, generally after RKC complete annual molting and mating in Bristol Bay. Fishing has occurred during the first 2 weeks of November each year since 1990. Thus, a lag of about 4.8 months, or 0.4 years, between abundance assessment and the fishery was used in our simulations.

S-R data for Bristol Bay RKC were also obtained from Zheng et al. (1995b) and were used to fit a four-parameter Ricker curve that combined two special cases of the general S-R model: a general Ricker curve that attributes change in recruitment to size of effective spawning biomass ($r_1 > 1$ and $a_1 = 0$; Appendix) and an autocorrelated Ricker curve that emphasizes recruitment changes as due to environmental causes ($r_1 = 1$ and $a_1 > 0$). The combined curve (Fig. 1) fit the data well ($R^2 = 0.62$, $df = 15$) and was used to conduct our simulations. Because the combined curve synthesizes two different, but potentially valid, interpretations of the data, sensitivity of the robust harvest strategy to these extremes was examined. Sex ratio of recruits was assumed to be 1:1.

Harvest model

Harvest procedure included comparison of stock status to threshold level, determination of a catch quota for legal crab, and estimation of deaths of sublegal and female crab due to handling. Annual effective spawning biomass, SP_t , was used to determine whether the population was above the threshold, T . If $SP_t \leq T$, then no fishing is allowed; otherwise, legal male harvest rate applied to legal crab (≥ 135 mm CL), NL_t , is

$$(1) \quad H_t = \min[E(NM_t/NL_t), MH]$$

where E is mature male harvest rate applied to NM_t , mature male abundance (≥ 120 mm CL), and MH is maximum legal male harvest rate. Catch by length of legal male crab (≥ 135 mm CL) is

$$(2) \quad C_{l,t} = H_t(N_{l,t} + O_{l,t})$$

and total yield (TC_t) is obtained by multiplying by the corresponding weight at length and summing over all lengths:

$$(3) \quad TC_t = \sum_l [C_{l,t} W_l], \quad l \geq 135 \text{ mm CL.}$$

Handling mortality was incorporated in the length-based model for female and sublegal male crab. We assumed that catchability for large

Table 1. Population parameters for a length-based model of Bristol Bay RKC (Zheng et al. 1995b) (see text and Appendix for parameter definitions).

Mid-CL (mm)	Weight (kg)		α_1		Max. female mates/male	Male molting probability
	Male	Female	Male	Female		
92.5		0.564		8.271	0.0	
97.5	0.696	0.634	28.902	7.734	0.0	0.980
102.5	0.815	0.709	28.902	7.197	0.0	0.969
107.5	0.948	0.789	28.902	6.660	0.0	0.953
112.5	1.094	0.873	29.287	5.800	0.0	0.928
117.5	1.256	0.962	29.480	5.048	0.0	0.893
122.5	1.432	1.056	29.480	4.511	1.0	0.842
127.5	1.625	1.155	29.672	4.189	1.2	0.773
132.5	1.835	1.258	29.865	3.867	1.4	0.686
137.5	2.063	1.367	30.058	3.437	1.6	0.583
142.5	2.310	1.480	30.250	2.148	1.8	0.472
147.5	2.576		30.443		2.1	0.364
152.5	2.862		30.636		2.4	0.264
157.5	3.169		30.829		2.7	0.190
162.5+	3.498		31.021		3.0	0.131

	Growth parameter			Natural mortality	
	Male	Female		Male	Female
<i>a</i>	13.14	16.49	Low	0.23	0.32
<i>b</i>	0.018	-0.097	High	1.04	1.72
β	0.519	0.931			

	S-R relationship					
	Ricker model			Proportion by length		
	General	Autocorrelated	Combined		Male	Female
<i>r</i> ₁	2.332	1.000	1.880	α_r	54.115	303.325
<i>r</i> ₂	-11.403	0.523	-7.396	β_r	1.885	0.313
<i>r</i> ₃	6.49×10^{-5}	2.05×10^{-5}	4.86×10^{-5}			
<i>k</i>	7.000	7.000	7.000			
<i>a</i> ₁	0.000	0.600	0.340			
σ	0.700	0.700	0.700			

(≥90 mm CL) female and sublegal (95–134 mm CL) male crab was 50% of that for legal male crab. This value is close to observed by-catch rates in the Bristol Bay RKC fishery in 1990 and 1991 (Beers 1991, 1992). Thus, female deaths due to handling were assumed to be

$$(4) \quad HD_{i,t} = 0.5 H_i F_{i,t} HM$$

where HM is bycatch mortality rate. Deaths from handling for sublegal males are obtained by replacing female abundances with sublegal male abundances in eq. 4. Therefore, magnitude of handling mortality is a function of harvest rate and bycatch mortality rate.

To account for handling mortality of female crab, effective spawning biomass was updated after fishing by modifying eq. A6 to deduct handling mortality from female abundance:

$$(5) \quad SP_t = r_t \sum_l [(F_{l,t} - HD_{l,t}) WF_l], \quad \iota \geq 90 \text{ mm CL.}$$

Handling mortality for sublegal male crab was included in equations for male abundance by replacing catch, $C_{l,t}$, with deaths due to handling for $\iota = 95\text{--}134$ mm.

Population abundances and effective spawning biomasses were estimated with measurement error. Measurement error was assumed to be log-normally distributed (Zheng et al. 1993) with a coefficient of variation (CV) of 0.2. This was estimated for Bristol Bay legal RKC abundances using a bootstrapping approach with our length-

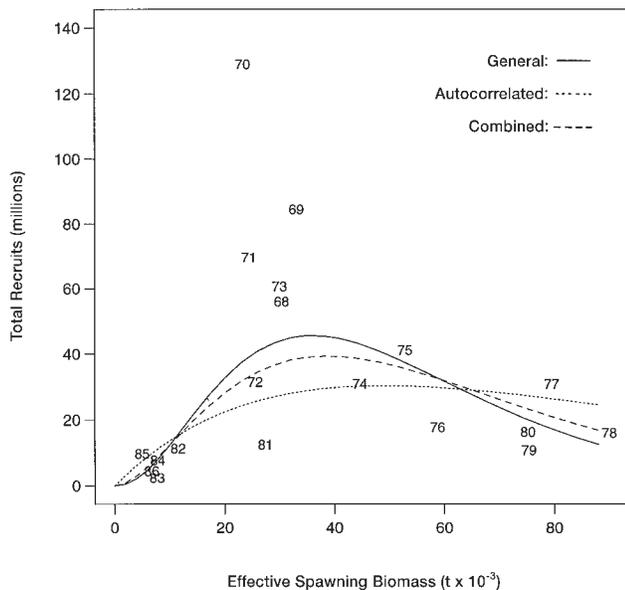
based model (Zheng et al. 1995b). We assumed that implementation error was zero because a previous study on herring thresholds showed that implementation error is not important to optimal threshold levels (Zheng et al. 1993).

Simulations

Harvest strategies for Bristol Bay RKC were analyzed through computer simulations of population dynamics under different scenarios of threshold levels and harvest rates for the combined S-R curve. Based on previous experience (Zheng et al. 1993), we expected that optimal threshold levels would likely range from 0 to 50% of SP_{∞} . The current threshold is about 15% of SP_{∞} . The current harvest rate for mature male crab is 20%, but 10–40% is likely to cover the range of reasonable alternatives. Currently, the maximum legal male harvest rate is 60%, but reasonable alternatives may range from 40 to 80%. Simulated horizon was set as 5200 years, and statistics were collected only in the last 5000 years to reduce effect of initial conditions on results. Because we were interested in long-term population dynamics, we used a single replicate with a long horizon to estimate evaluation criteria. We evaluated each level of threshold and harvest rate in the simulations by a grid method. The grid interval was 5% for thresholds and mature male harvest rates and 10% for maximum legal male harvest rates.

The SP_{∞} was estimated as the mean of effective spawning

Fig. 1. Relationships between total recruits at age 6.2 years (i.e., 7-year time lag) and effective spawning biomass for Bristol Bay RKC. Numbers refer to brood year. The data are from Zheng et al. (1995b).



biomasses without fishing under average environmental conditions. To ensure a stable estimate of SP_{∞} , simulated horizon was increased to 50 200 years and statistics in the last 50 000 years were used.

Currently, data are not available to estimate mortality of sublegal (95–134 mm CL) male and large (>89 mm CL) female RKC that are handled during commercial fisheries. Three handling mortality rates for crab bycatch were examined in this study: 0, 20, and 50%.

Three kinds of mechanisms are likely to cause a population collapse: a sudden increase in natural mortality, poor recruitment for an extended period, and overfishing. We introduced these mechanisms in the simulations by including time-variable natural mortality in the population model, autocorrelated recruitment in the S–R model, and high harvest rates up to 40% of mature male abundance in the harvest model.

Natural mortality for Bristol Bay RKC changes over time (Zheng et al. 1995b). Causes for this change are unknown, and we assumed that it is triggered by environmental conditions. Many environmental factors fluctuate with a cycle period from 12 to 24 years (Hollowed and Wooster 1992). Thus, we assumed two constant levels of instantaneous natural mortality (low and high, Table 1) with a cycle duration lasting 12–24 years: a low mortality for 10–20 years and then a switch to high mortality lasting for 2–4 years. Durations for these periods were set randomly. Natural mortality patterns of RKC in Bristol Bay during the last two decades were similar to this scenario (Zheng et al. 1995b). A sensitivity study was conducted to examine effects of 10 different scenarios of natural mortality (Table 2) on a robust harvest strategy.

Simulations were initialized with a crab population of 50 million males (>94 mm CL) and 50 million females (>89 mm CL), an intermediate population size for the past 20 years. Length frequency distribution of the initial population was assumed that of Bristol Bay RKC in 1972. Identical seeds for random number generators were used for all scenarios to compare different harvest strategies under the same environmental conditions.

Evaluation criteria

Threshold management strategies for Bristol Bay RKC seek to protect stock reproductive potential and to achieve maximum long-term yield

(NPFMC 1990; Pengilly and Schmidt 1995). These two objectives are related. If the stock is depressed, it is impossible to achieve maximum long-term yield. Conversely, maximum long-term yield is probably obtained when reproductive potential is optimal. A simple objective function described by Quinn et al. (1990) provides a tradeoff between long-term yield and variability in yield:

$$(6) \quad \max [((1-\lambda)Y_i - \lambda SD_i)]$$

where Y_i and SD_i are mean and standard deviation of yield under management policy i and λ is a penalty weighting factor that measures the cost of one unit increase in variability in yield in terms of mean yield. Two special cases of this objective function are maximum mean yield ($\lambda = 0$) and equal tradeoff between mean yield and variability in yield ($\lambda = 0.5$). We used this objective function with $\lambda = 0$ and 0.5 as the primary criterion to estimate optimal threshold levels, mature male harvest rates, and maximum legal male harvest rates. Additional evaluation criteria included loss of harvest opportunity, expressed as a percentage of years the fishery is closed, and variability in effective spawning biomass.

Results

Pristine effective spawning biomass

Pristine effective spawning biomass was estimated using each of three S–R relationships to allow comparative sensitivity analyses. The general Ricker curve resulted in the highest SP_{∞} (45 885.7 t) followed by the combined Ricker curve (43 949.3 t). The autocorrelated Ricker curve produced the lowest SP_{∞} (36 720.8 t). The SP_{∞} for the general Ricker curve and combined curve are higher because influence of strong year-classes at intermediate levels of effective spawning biomass is greater for these curves than the autocorrelated Ricker curve. Given the observed biomasses during the last two decades of extensive harvests, estimated SP_{∞} for the autocorrelated Ricker curve may be too low.

Tradeoffs of using a threshold

Tradeoffs of different threshold levels under the current mature male harvest rate of 20% and maximum legal male harvest rate of 60% are illustrated in Fig. 2. With a handling mortality rate of 20% or less, effects of threshold on mean yield and variability in spawning biomass were very minor. However, increasing thresholds reduced fishing opportunity and increased annual variability in yield. Thus, there appears to be some cost but little benefit for using a threshold under these harvest rates and handling mortality rates. Under the scenario with a handling mortality rate of 50%, a threshold was important to protect the population and enhance long-term yield. Mean yield increased, and variability in effective spawning biomass was greatly reduced when a threshold was increased above 20% of SP_{∞} . With a handling mortality rate of 50%, a threshold at or above 20% of SP_{∞} was required to prevent population collapse to zero abundance.

Optimal combinations of thresholds and mature male harvest rates

Optimal combinations of threshold levels and mature male harvest rates were evaluated for the current maximum legal harvest rate of 60% (Fig. 3). Objective function values were scaled to a maximum value of 1 and contours of values plotted as a function of threshold level and mature male harvest rate for each combination of weighting factor and handling mortality

Table 2. Period lengths, low and high values of natural mortality (*M*), and associated pristine effective spawning biomass (*SP_∞*) for 10 scenarios (A–J) of natural mortality used to evaluate the robust harvest strategy for Bristol Bay RKC (each scenario specifies a low and a high *M* and corresponding period lengths).

Scenario	High period (years)	Low period (years)	Low <i>M</i>		High <i>M</i>		<i>SP_∞</i> ($t \times 10^{-3}$)
			Male	Female	Male	Female	
A	Constant over time		0.23	0.32	0.23	0.32	62.480
B	Constant over time		0.29	0.49	0.29	0.49	49.546
C	Constant over time		0.41	0.62	0.41	0.62	39.958
D	1–3	11–21	0.23	0.32	1.04	1.72	50.312
E	2–3	10–21	0.23	0.32	1.04	1.72	48.219
F	2–4	10–20	0.23	0.32	1.04	1.72	45.886
G	2–5	10–19	0.23	0.32	1.04	1.72	43.674
H	3–5	9–19	0.23	0.32	1.04	1.72	41.662
I	3–6	9–18	0.23	0.32	1.04	1.72	39.460
J	4–6	8–18	0.23	0.32	1.04	1.72	37.160

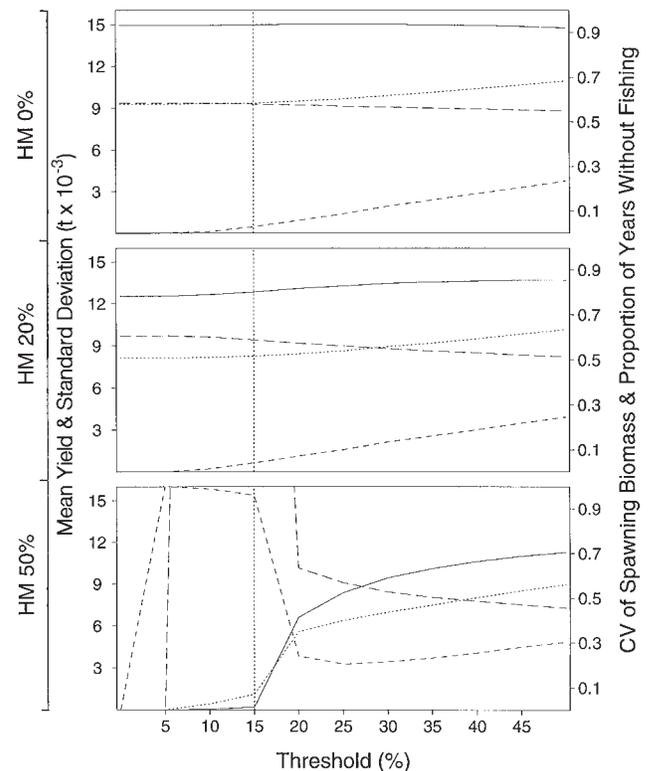
rate. With the maximum mean yield criterion ($\lambda = 0.0$), optimal threshold levels were 50% and optimal mature male harvest rates were negatively related to handling mortality rate (Fig. 3). For handling mortality rates of 0, 20, and 50%, optimal mature male harvest rates were 35, 25, and 20%, respectively. Without handling mortality, contour lines were flat across different threshold levels, indicating that a threshold was not needed. For high handling mortality rates (50%), contours were generally separated as two regions: an upper left region where high mature male harvest rate and low threshold level drove the population to collapse and a middle right region where a high threshold level helped achieve high yield. Between these two regions, yield changed dramatically (Fig. 3).

With the equal tradeoff criterion ($\lambda = 0.5$), optimal threshold levels varied from 10 to 25% under all scenarios (Fig. 3). Increased handling mortality rate reduced optimal mature male harvest rate. At low handling mortality rates ($\leq 20\%$), objective function values were generally not affected by threshold levels between 0 and 25% as long as mature male harvest rates were close to 15–20% (Fig. 3).

The current harvest strategy achieves >85% of maximum objective function values possible with either maximum mean yield or equal tradeoff criterion if handling mortality rates are $\leq 20\%$ (Fig. 3). The current harvest strategy is located near or at a very steep area of response surfaces with higher handling mortality rates ($\geq 20\%$) and results in less than 30% of maximum objective function values with a 50% handling mortality rate (Fig. 3). Thus, risk of population collapse is high under uncertainty of handling mortality or unfavorable environmental conditions if more than half the crab that are returned to the sea due to sex or size restrictions die.

Either lower mature male harvest rates or higher threshold levels would reduce this risk. Lower mature male harvest rates would reduce mean yields under scenarios of low handling mortality (0–20%), but yields would be less sensitive to threshold level than those under the current mature male harvest rate. Higher thresholds would increase objective function values for scenarios of high handling mortality rates, yet cause little or no change in objective function values for low handling mortality rate scenarios. Thus, a lower mature male harvest rate and higher threshold level is a robust strategy to produce high yield and low risk of population collapse under all possible handling mortality scenarios considered.

Fig. 2. Mean yield (solid lines), standard deviation of yield (dotted lines), percentage of years without a fishery (short-dashed lines), and CV of effective spawning biomass (long-dashed lines) as a function of threshold level (% pristine effective spawning biomass) for Bristol Bay RKC under the current 20% mature male harvest rate and 60% maximum legal male harvest rate. Plots are classified by 0, 20, and 50% handling mortality rate (HM). Vertical dotted lines correspond to the current threshold level.

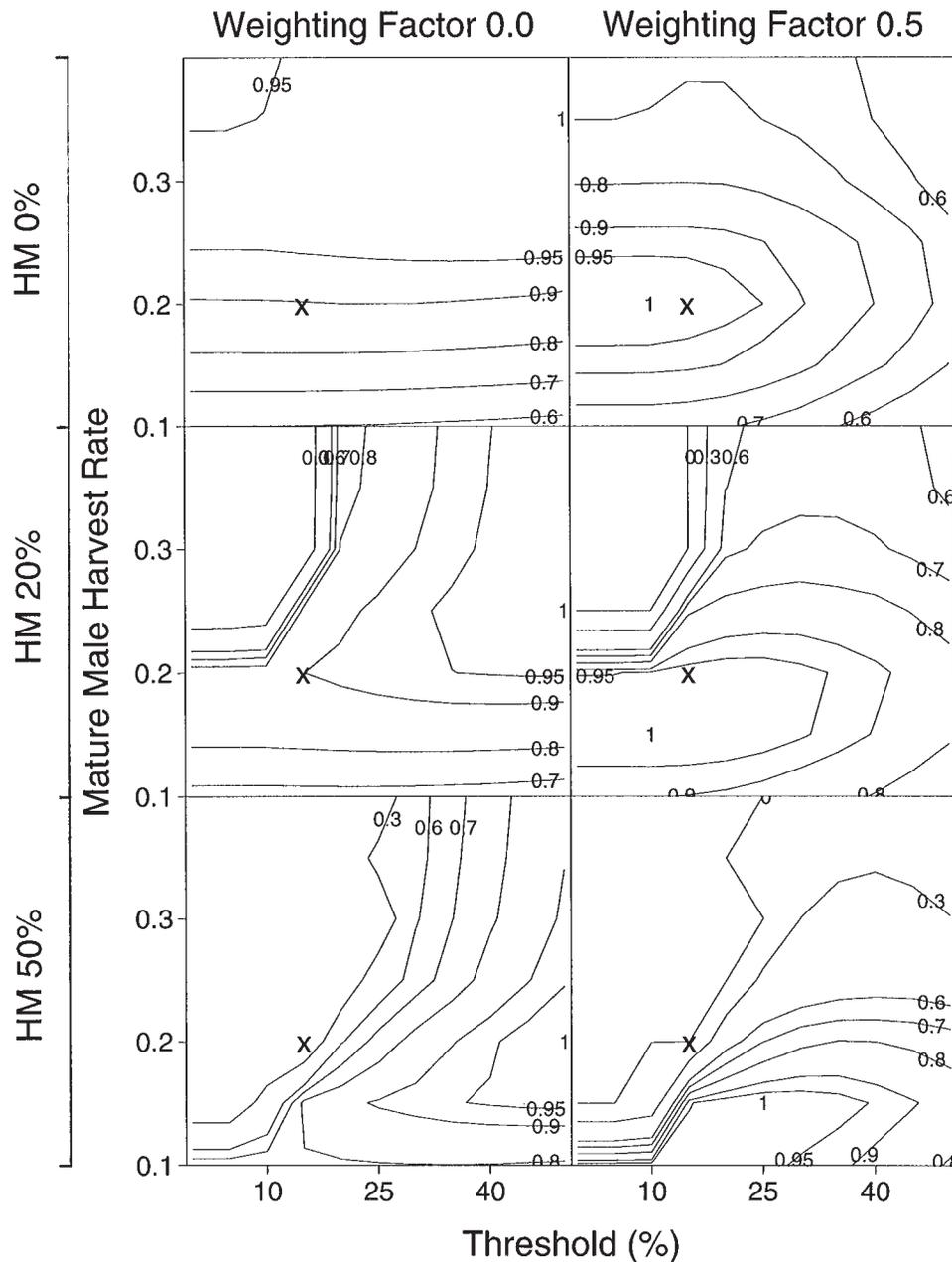


Optimal maximum legal male harvest rates

Next, we evaluated optimal maximum legal male harvest rates under alternative mature male harvest rates and thresholds. Optimal maximum legal male harvest rates were most dependent on management objectives and handling mortality (Fig. 4).

For the maximum yield criterion, maximum mean yields increased slightly when maximum legal male harvest rates

Fig. 3. Contour plots of the objective function by threshold level and mature male harvest rate for a 60% maximum legal male harvest rate for Bristol Bay RKC. Plots are classified by two weighting factors, $\lambda = 0$ and $\lambda = 0.5$, and 0, 20, and 50% handling mortality rates (HM). \times = current harvest strategy.



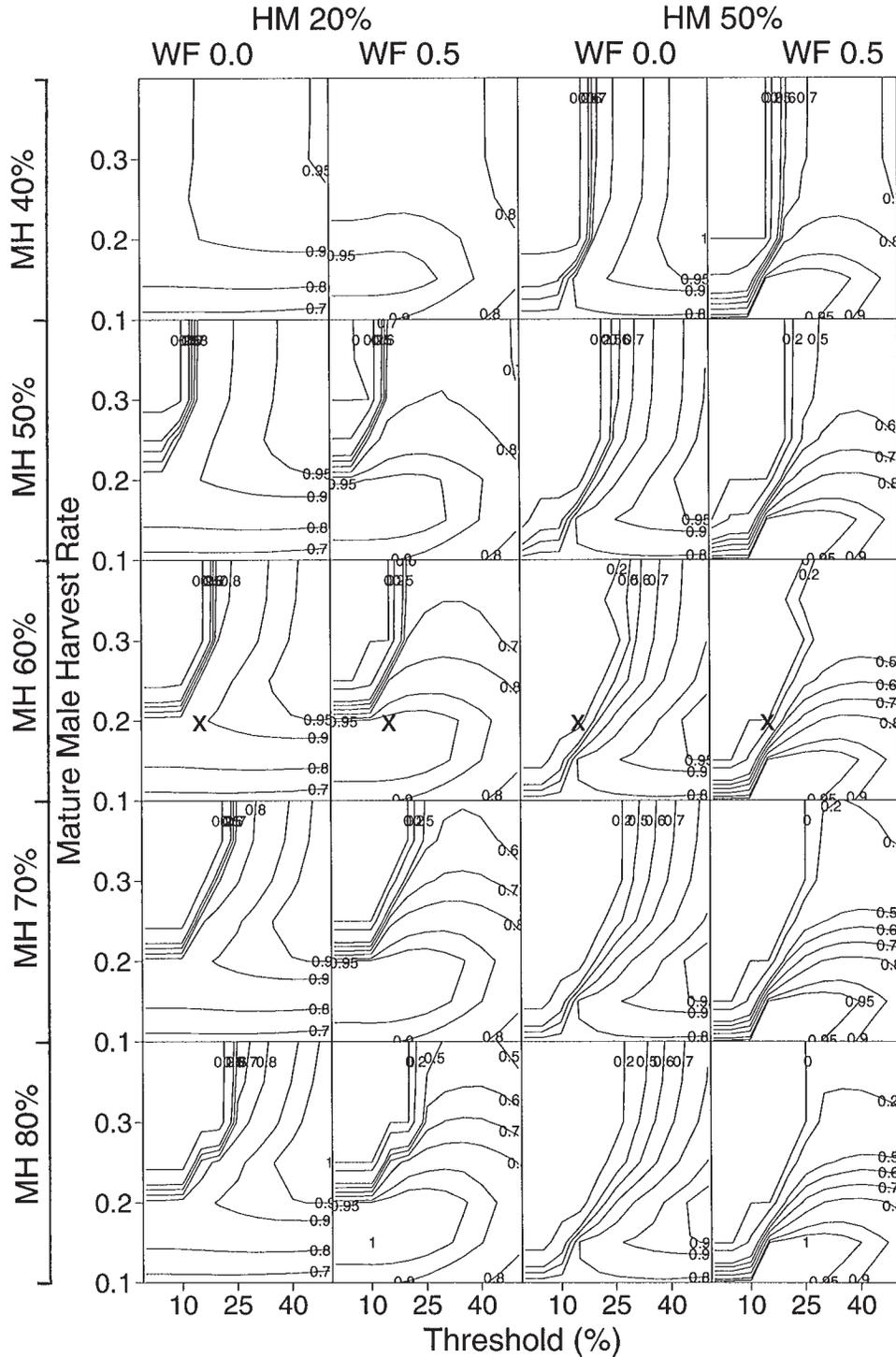
increased from 40 to 80% with a handling mortality rate of 20%. With a handling mortality rate of 50%, the maximum mean yield occurred with a maximum legal male harvest rate of 40% (Fig. 4). For both 20 and 50% handling mortality rates, response surfaces became flatter by decreasing maximum legal male harvest rates from 80 to 40%. Under all scenarios but one (20% handling mortality rate and 40% maximum legal male harvest rate), combinations of high mature male harvest rates and low threshold levels caused population collapse. The region susceptible to collapse increased with increasing maximum legal male harvest rate.

For the equal tradeoff criterion, maximum objective function

values occurred with a maximum legal male harvest rate of 80% for both 20 and 50% handling mortality rates (Fig. 4). Response surfaces generally became flatter as maximum legal male harvest rates decreased from 80 to 40%.

Overall, for both criteria, a maximum legal male harvest rate of 40 or 50% generally resulted in a broader region for high objective values and a narrower region of population collapse than with maximum legal male harvest rates $\geq 60\%$. Maximum objective values were higher under a 50% maximum legal male harvest rate than under a 40% rate for both 20 and 50% handling mortality rates. Therefore, a maximum legal male harvest rate of 50% is the best choice.

Fig. 4. Contour plots of the objective function by threshold level and mature male harvest rate for Bristol Bay RKC. Plots are classified by 0.0 and 0.5 weighting factors (WF), 20 and 50% handling mortality rates (HM), and 40, 50, 60, 70, and 80% maximum legal male harvest rates (MH). × = current harvest strategy.



Optimal combinations of mature male and maximum legal male harvest rates and thresholds

Choice of management objective and handling mortality rate affected optimal combination of mature male harvest rate, maximum legal male harvest rate, and threshold. For the maximum yield criterion, both optimal mature male harvest rate and

optimal maximum legal male harvest rate doubled when handling mortality rate decreased from 50 to 0% (Table 3). Optimal threshold levels were 50%, and the chance of fishery closure was greater than 28% under optimal strategies.

For the equal tradeoff criterion, optimal threshold levels increased from 10 to 25% and optimal mature male harvest

Table 3. Optimal mature male harvest rates (*E*), maximum legal male harvest rates (MH), threshold levels (TH), and associated mean yield and standard deviation of yield and percentage of the simulation years the fishery was closed for Bristol Bay RKC (HM = handling mortality rate).

HM (%)	Optimal						Current: <i>E</i> = 20%, MH = 60%			
	<i>E</i> (%)	MH (%)	TH (%)	Yield ($t \times 10^{-3}$)	SD ($t \times 10^{-3}$)	Closed (%)	TH (%)	Yield ($t \times 10^{-3}$)	SD ($t \times 10^{-3}$)	Closed (%)
Maximum yield criterion ($\lambda = 0$)										
0	40	80	50	17.958	15.780	32.2	25	15.001	9.649	8.6
20	25	80	50	14.386	11.332	28.5	45	13.659	9.822	21.8
50	20	40	50	11.438	9.119	28.7	50	11.263	8.957	30.4
Equal tradeoff criterion ($\lambda = 0.5$)										
0	20	80	10	15.005	9.194	0.7	10	14.934	9.309	0.7
20	15	80	10	11.870	7.055	0.6	20	13.071	8.429	7.1
50	15	80	25	10.213	6.419	10.5	35	10.095	7.482	23.2

Table 4. Comparisons of mean yield, standard deviation of yield, CV of effective spawning biomass (SP), percentage of years without fishing (closed), and ranges of closed and open durations by handling mortality rate (HM) for the current harvest strategy (20% mature male harvest rate, 60% maximum legal male harvest rate, and a threshold of 6600 t of effective spawning biomass) and the robust strategy (15% mature male harvest rate, 50% maximum legal male harvest rate, and a threshold of 11 000 t) for Bristol Bay RKC (historical mean yield and its standard deviation included for comparison).

HM (%)	Yield ($t \times 10^{-3}$)	SD ($t \times 10^{-3}$)	CV SP (%)	Closed (%)	Closed duration (years)	Open duration (years)
Current strategy						
0	14.965	9.371	58.1	2.8	1–3	1–177
20	12.839	8.270	58.9	4.0	1–4	1–238
50 ^a	3.098	2.951	79.8	38.6	1–9	1–16
Robust strategy						
0	12.888	8.038	56.3	7.6	1–5	1–173
20	12.080	7.478	55.1	8.1	1–6	1–173
50	10.280	6.528	54.5	10.3	1–5	1–101

Historical yield

Period	Yield ($t \times 10^{-3}$)	SD ($t \times 10^{-3}$)
1953–1994	13.907	13.169
1960–1994	15.737	13.705
1972–1994	15.031	15.788

^aThe population was not sustainable for this scenario. Statistics were computed using results before the population collapsed to zero abundance (493 years).

rates decreased from 20 to 15% when handling mortality rates increased from 0 to 50% (Table 3). Optimal maximum legal male harvest rate (80%) was not affected by handling mortality rate. Mean yield decreased 11–17% under the equal tradeoff criterion compared with that under the maximum yield criterion, but this loss was more than compensated by benefits of a 30–42% reduction in variability in yield and a 63–98% reduction in proportion of years without fishing.

When the maximum yield criterion was applied to the current 20% mature male harvest rate and 60% maximum legal male harvest rate, optimal threshold levels ranged from 25%

under scenarios of no handling mortality to 50% with a 50% handling mortality rate (Table 3). For all scenarios, yield was lower under current harvest rates than under optimal levels, especially for no or low handling mortality. Proportions of years without fishing were much more variable under current harvest rates than under optimal strategies for different scenarios of handling mortality.

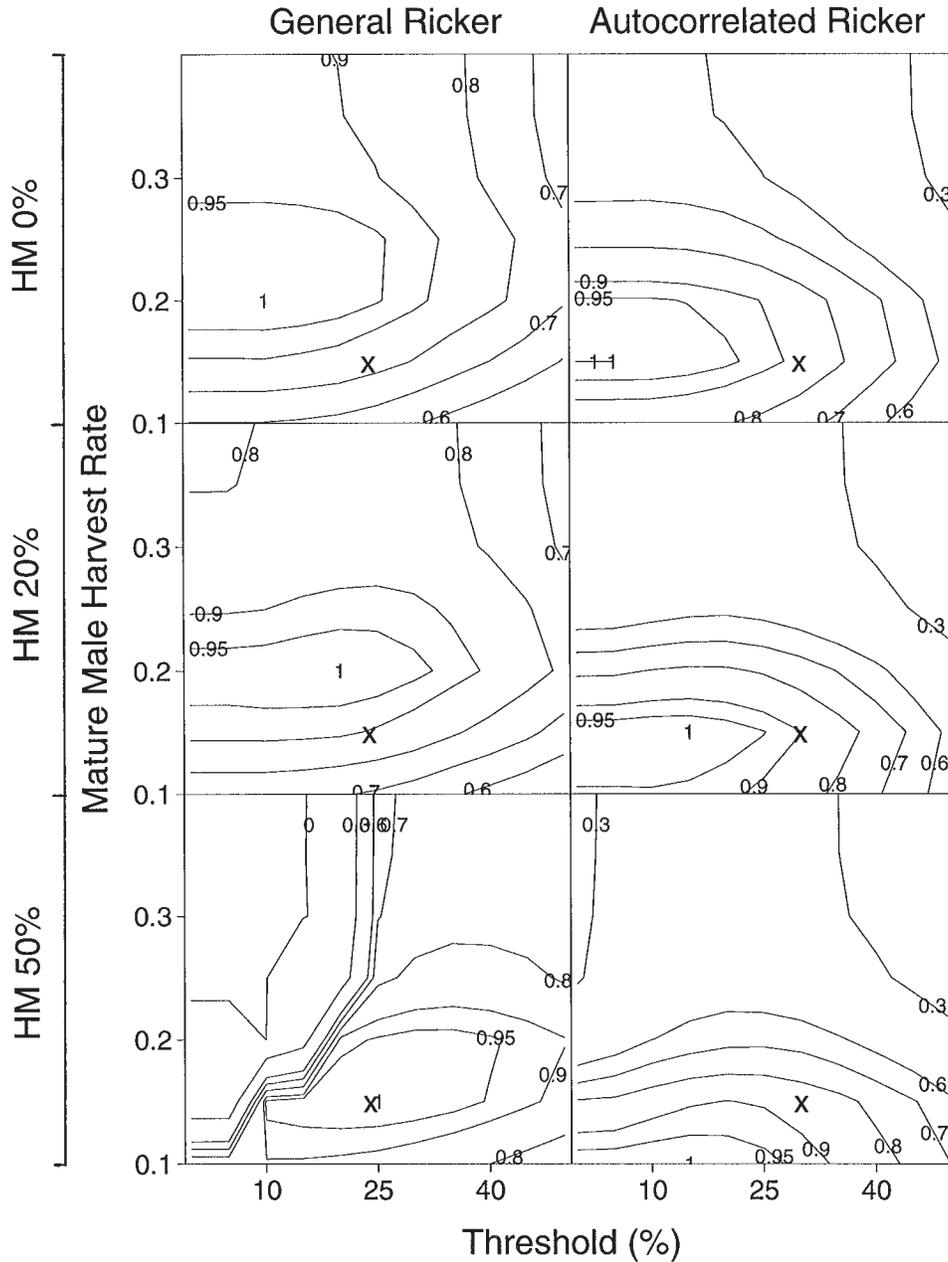
When the equal tradeoff criterion was applied to current harvest rates, optimal threshold levels increased from 10 to 35% as handling mortality rates increased from 0 to 50%. Proportions of years without fishing were much higher under current harvest rates than under optimal strategies for scenarios with handling mortality rates $\geq 20\%$.

A robust harvest strategy

From our results so far, we formulated a harvest strategy that is robust under uncertainties of recruitment and high natural and handling mortalities. Simulations indicated that a combination of a 15% mature male harvest rate, a 50% maximum legal male harvest rate, and a threshold level of 11 000 t (25%) of effective spawning biomass produced a high mean yield with low variability while providing protection of crab reproductive potential. The current mature male harvest rate of 20% is close to the mean rate from 1972 to 1978. Higher mature male harvest rates were observed after this time period during the late 1970s and early 1980s; this was followed by a precipitous decline in population abundance in the early 1980s (Zheng et al. 1995a). A maximum legal male harvest rate of 50% is lower than the current rate of 60%, but actual legal male harvest rates during 1972–1993 exceeded 50% only twice (Zheng et al. 1995a). Our results also showed that a 20% mature male harvest rate resulted in harvest of 47% of legal crab abundance, while a 15% mature male harvest rate produced a 32% legal male harvest rate. A threshold of 11 000 t is 67% higher than the current threshold level of 6600 t of effective spawning biomass (8.4 million mature females).

Mean yield was slightly higher with the current harvest strategy than for the robust strategy with scenarios of low handling mortality rates (Table 4). However, mean yield was much higher for the robust strategy than with the current strategy under scenarios with a high handling mortality rate (50%). Percentages of years without fishing were in general higher for the robust strategy than with the current strategy (Table 4). Variability in yield and effective spawning biomass was slightly lower for the robust strategy, so population production

Fig. 5. Contour plots of the equal tradeoff objective function by threshold level and mature male harvest rate for a 50% maximum legal male harvest rate for Bristol Bay RKC. Plots are classified by a general and an autocorrelated Ricker S–R curve and 0, 20, and 50% handling mortality rates (HM). × = robust harvest strategy (15% mature male harvest rate, 50% maximum legal male harvest rate, and a threshold of 11 000 t).



was more stable. Actual variability in yield during the last four decades was higher than results from our simulation study (Table 4) because historical harvest rates changed over time.

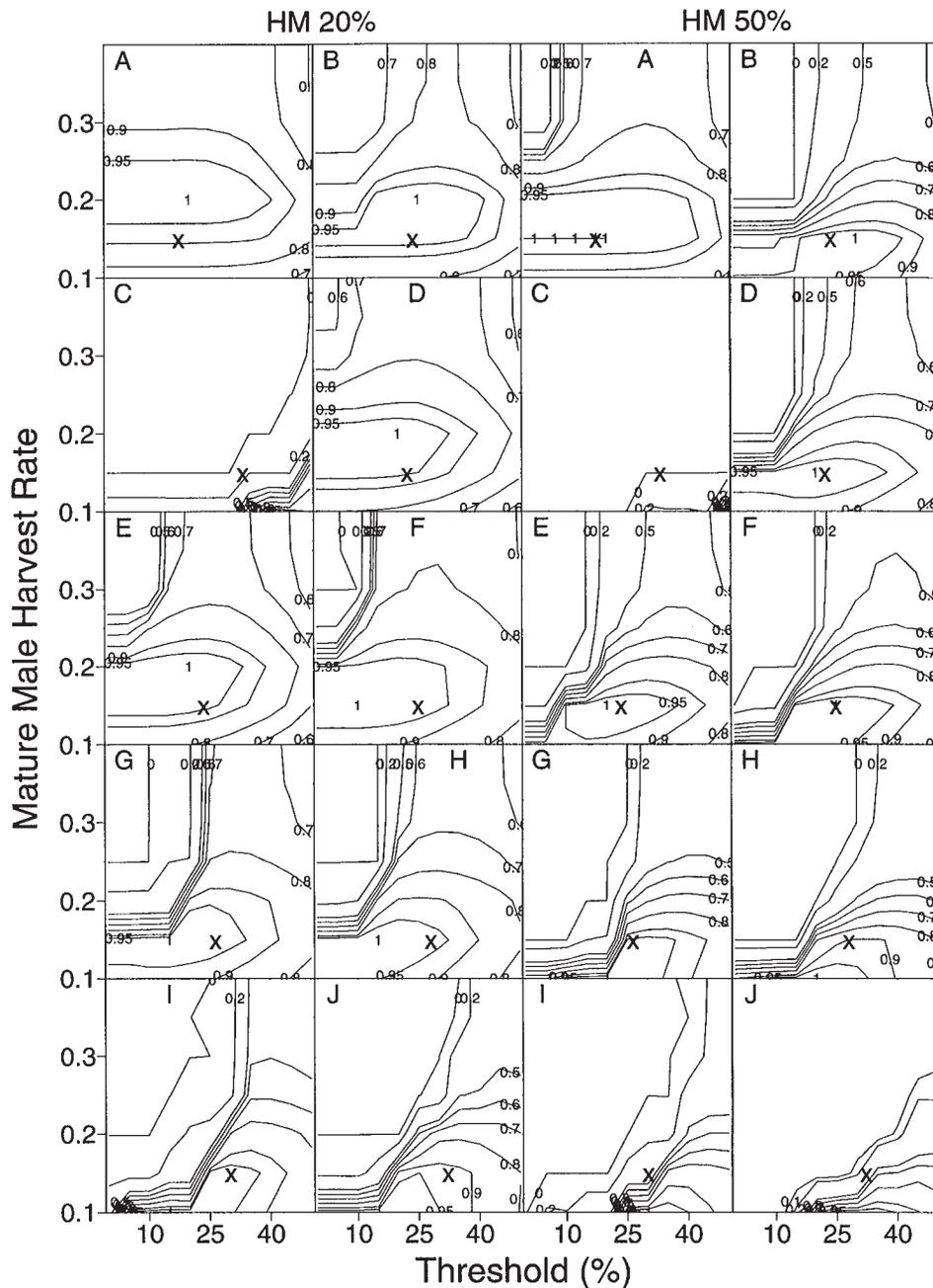
Sensitivity of robust harvest strategy to dynamics of S–R curves, natural mortality, and handling mortality

Sensitivity of the robust harvest strategy to dynamics of S–R relationships was examined using the equal tradeoff criterion for the general Ricker curve and autocorrelated Ricker curve (Fig. 5). As expected, results from these two S–R curves bracket our results from the combined curve (Fig. 3, right-hand panels) that includes both density-dependent and autocorrelated

environmental effects. Overall, benefits of a threshold to long-term yield and population conservation were greater with the general Ricker curve than with the autocorrelated Ricker curve because recruitment success with the former is more influenced by spawning stock. With the general Ricker curve, the stock was much more vulnerable to overfishing under high handling mortality rates. Under all scenarios considered, the robust harvest strategy was located in or near flat areas of the response surfaces and produced more than 80% of the possible maximum objective function values (Fig. 5).

Interannual variation of natural mortality is still a major source of uncertainty in a simulation study to evaluate crab

Fig. 6. Contour plots of the equal tradeoff objective function by threshold level and mature male harvest rate for Bristol Bay RKC. Plots are classified by 20 and 50% handling mortality rates (HM) and 10 scenarios (A–J) of natural mortality (see Table 2). × = robust harvest strategy.



harvest strategies. Effects of natural mortality on the robust harvest strategy were examined with the equal tradeoff criterion and the combined S–R curve for 10 different scenarios of natural mortality (Table 2), ranging from very low to extremely high mortality (Fig. 6). With a 20% handling mortality rate, the strategy was very robust to natural mortality and achieved more than 90% of maximum objective values possible for all scenarios except scenario C (Fig. 6). With a 50% handling mortality rate, the strategy was robust to all except three high natural mortality scenarios, C, I, and J (Fig. 6). The likelihood that a 50% handling mortality rate has occurred with one of these high natural mortalities during the history of this

fishery is low because this combination would result in mortality rates much higher than the mean mortality rate that we estimated over the past three decades (Zheng et al. 1995a, 1995b). Thus, it appears that the robust harvest strategy would result in 90% or more of the possible maximum objective function values under likely scenarios of natural mortality.

Last, we compared the performance of the robust harvest strategy and current harvest strategy with respect to uncertainty of handling mortality rate (Fig. 7). The robust strategy was located in the relatively flat area of the response surface over all handling mortality rates. When handling mortality rates were <70%, the robust strategy achieved more than 60%

of the maximum objective function values possible. In comparison, objective function values declined dramatically when handling mortality rates exceeded 30% under the current harvest strategy (Fig. 7). For a given mature male harvest rate, a high handling mortality rate needs to be compensated with a high optimal threshold level that functions as an alternative means to reduce total fishing mortality. Handling mortality rate is thus a key factor in determining optimal threshold level for a given mature male harvest rate.

Discussion

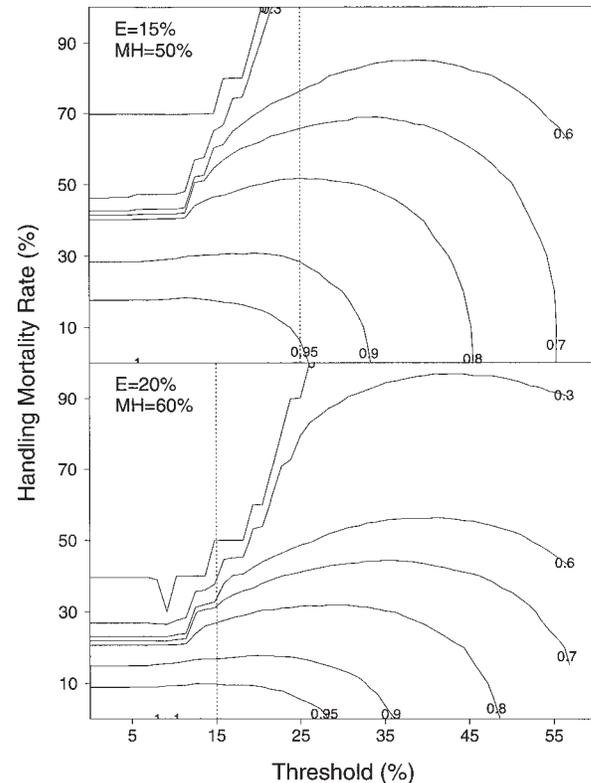
A harvest strategy for a fishery is highly dependent on both management objectives and recruitment dynamics of the population (Quinn et al. 1990; Zheng et al. 1993). When the objective is to maximize yield, optimal harvest strategy is both a high harvest rate and a high threshold level. Together, these cause pulse fishing, with corresponding high variability in yield and economic instability. On the other hand, when low variability in yield is as important as mean yield level, optimal harvest rate and threshold level must be set at intermediate levels. Although mean yield is slightly less than maximum yield for an equal tradeoff objective, lower harvest rates reduce variability in yield and the fishery is closed much less often. Use of a threshold helps to conserve a population, enhance long-term yield, and provide management flexibility.

The Alaska Board of Fisheries policy on king crab management is best approximated by the equal tradeoff criterion in which yield and variability in yield are weighted equally (ADF&G 1994). Among other objectives, the policy strives to provide for a sustained and reliable supply of high-quality product, substantial and stable employment, minimum risk of stock collapse, and maintenance of fisheries on multiple ages and sizes of crab. The Board recognized that this policy "may not result in maximization of physical or economic yield" (ADF&G 1994).

We assumed a low level of first-order autocorrelation for the combined S-R curve. However, if RKC recruitment in Bristol Bay is not only dependant at low stock sizes but is more strongly autocorrelated than we assumed, then we have underestimated the frequency of population collapses and the length of time that the population is depressed. One mechanism for strong autocorrelation could be a sudden switch from favorable to unfavorable environmental conditions and vice versa, where each trend continues for a long time, e.g., from 6 to 12 years (Hollowed and Wooster 1992). In such cases, a high threshold is required to save enough spawning stock until favorable environmental conditions occur. Although we did not examine such strong recruitment autocorrelations, we found that a threshold management strategy is optimal when similar cycles occur in natural mortality. Effects of environmental conditions on recruitment of Bristol Bay RKC are currently being investigated (Tyler and Kruse 1996), and results should be incorporated into future studies of harvest strategies.

Handling mortality reduces future recruitment to the fishery by reducing both survival of prerecruits and effective spawning biomass due to deaths of mature females and sublegal males. Besides mortality, handling may also produce sublethal effects on crab such as reduced growth (Kruse 1993). To estimate handling mortality, we assumed a 50% catchability for sublegal male and large female crab, based on overall observed

Fig. 7. Contour plots of the equal tradeoff objective function by threshold level and handling mortality rate with 15 and 20% mature male harvest rates (E) and 50 and 60% maximum legal male harvest rates (MH) for Bristol Bay RKC. Vertical dotted lines correspond to threshold levels for the robust (upper plot) and current (bottom plot) harvest strategies.



bycatch rates for the Bristol Bay RKC fishery in 1990 and 1991 (Beers 1991, 1992). However, bycatch catchability in 1992 and 1993 was near 100% (Tracy 1994). Increased bycatch catchability is probably attributable to reduced soak time resulting from shorter fishing periods and 250-pot limit per boat starting in 1992. Increase of pot mesh size from 19.7 to 22.9 cm for at least one third of one vertical surface of pot, starting in 1995, may nullify the effect of pot limitation and result in a bycatch catchability closer to 50%. If bycatch catchability is higher than 50%, total mortality rate for prerecruits and large females is underestimated in our study. Furthermore, crab near legal size may be more likely to be caught as bycatch. Unfortunately, data to compute length-dependent catchability were unavailable.

We examined a wide range of handling mortality rates for Bristol Bay RKC. Handling mortality rates may depend on handling injury, air temperature, wind speed, shell condition, and numerous other factors (Kruse 1993; Murphy and Kruse 1995). Exposure of RKC to cold air reduces vigor, lowers growth, and leads to increased mortality during ecdysis in severe situations (Carls and O'Clair 1990). Such effects could be significant during extremely cold weather during winter fisheries in some years. We estimated that average exposure of RKC to cold air during November fisheries during cold years would be milder than -1 C degree-hour which leads to handling mortality rates of 20% or less (Carls and O'Clair

1990). Unwanted crab are normally returned to the sea within 4 min (Zhou and Shirley 1996), and the coldest mean November air temperature at St. Paul, Alaska (near fishing grounds), during the history of the fishery was -2.1°C in 1987. However, historically the fishery extended longer into January through March when cold air exposure is more severe. Further, chill effects due to high wind in some years may cause higher handling mortality rates.

On the other hand, simulated deck and water impacts caused no increase in mortality of RKC, although injuries to spine and rostrum increased with handling (Zhou and Shirley 1995, 1996). Water impact was dismissed as a cause of mortality because recovery rates of tagged RKC during the fishery in 1993 were not significantly different among release methods (Watson and Pengilly 1994).

Not all potential factors contributing to handling mortality have been adequately studied (Kruse 1993; Murphy and Kruse 1995), so the level of handling mortality experienced in the Bristol Bay RKC fishery remains uncertain. For instance, effects of handling and habitat dislocation on predation mortality are unknown. Further, some crab receive abnormal treatment (e.g., dropped from height on deck, stepped on, left on deck for long periods) that may cause death or increase susceptibility to disease and subsequent death. Given uncertainties, we believe that handling mortality rates of 10–20% may be a reasonable assumption for purposes of our analysis. We have considered handling mortality rate as high as 50% to gauge potential handling effects that might have occurred historically in some years or from other effects that have yet to be corroborated by research. For frame of reference, the combination of a 50% catchability, 40% legal male harvest rate, and 50% handling mortality rate causes a 10% annual handling mortality rate for sublegal male and large female crab in the population.

Because of its importance to management strategy, we recommend the following research on handling mortality. First, ongoing collection and analysis of observer data provide improved estimates of bycatch catchability for female and sublegal male crab in response to changing regulations and fishing techniques. Second, air temperatures and wind speeds during the history of the fishery could be analyzed with respect to records of dead crab in landings statistics to estimate the significance of cold air exposure to stock declines. Third, effects of handling and habitat dislocation on predation mortality need to be specifically investigated. Finally, an alternative approach is to design a crab pot that reduces bycatch catchability, thereby minimizing handling mortality rate.

We did not evaluate two important aspects of the current harvest strategy for Bristol Bay RKC: size limits and sex restrictions. Thus, harvest strategies that we obtained may be still suboptimal. Large male crab get a higher price per unit of weight than small male crab (Bibb and Matulich 1994). In addition, processors avoid smaller crab because processing costs per pound vary inversely with crab size and because presence of smaller crab on the market depresses the price of larger crab (Bibb and Matulich 1994). Similarly, there is less economic incentive to harvest female crab which are smaller on average than the majority of male crab. Therefore, size limits and sex restrictions are based not only on considerations of stock spawning biomass, but also on fishery economics.

Handling mortality is linked to size and sex restrictions. Harvest of females and reduction of male size limit would

reduce handling mortality and lead to lower optimal threshold levels. However, to develop an optimal “keep what you catch” harvest strategy with minimal bycatch would require a dynamic, bioeconomic model that incorporates size–price data by sex that are currently unavailable. Moreover, future bioeconomic analyses of female harvests should incorporate structural shifts in market economics resulting from potential sales of live, roe-bearing crab.

Given current size limits and sex restrictions, we recommend changing the current harvest strategy by reducing mature male harvest rate from 20 to 15% and maximum legal male harvest rate from 60 to 50%. Based on our belief that handling mortality rates may be 10–20% or so, no change in the current threshold level is warranted. However, if concerns exist that handling mortality rate is greater than 30%, the threshold level needs to be increased from 6600 to 11 000 t of effective spawning biomass. Our recommended strategy is robust to the uncertainties in handling mortality, S–R relationship, and environmental effects on recruitment and natural mortality that we examined in this study.

RKC tend to have life history traits that are identified with the stereotype of a *K*-selected species (Kruse 1993). High age-at-maturity, low frequency of strong year-classes, time-variable natural mortality, and compact aggregations render RKC exceptionally vulnerable to recruitment overfishing. Once the population collapses, it may take a long time to recover. If year-class strengths are affected by depensatory predation mortality, as evidenced by the general S–R relationship (Blau 1986; Zheng et al. 1995a), recovery of depressed stocks is difficult. A decade after the two largest RKC populations in Alaska crashed, Bristol Bay RKC are still at historically low levels and Kodiak RKC have not shown signs of recovery.

If population collapse is not due to overfishing, it may be impossible for any management strategy to prevent population collapse. However, since overfishing may possibly be a cause of collapse, it is prudent to minimize chance of collapse by preventing overfishing through harvest controls. When combined with harvest rate strategy, the threshold approach enhances long-term yield and is robust to management errors and uncertainties in population dynamics and environmental effects.

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Appendix. Population model for Bristol Bay red king crab

The following model was applied to male crab. The female model is the same except that catch was replaced by handling mortality, and molting probability was set equal to 1.0. Abundances by length and shell condition in any one year result

from abundances the previous year minus fishing, handling and natural mortality, plus recruitment and additions to or losses from each length-class due to growth:

$$(A1) \quad N_{l+1, t+1} = \sum_{l'=l+1}^{l+1} [P_{l', t+1} ((N_{l', t} + O_{l', t}) e^{-M_t} - C_{l', t} e^{(y-1)M_t}) m_{l'}] + R_{l+1, t+1}$$

$$O_{l+1, t+1} = ((N_{l+1, t} + O_{l+1, t}) e^{-M_t} - C_{l+1, t} e^{(y-1)M_t}) \times (1 - m_{l+1})$$

where $N_{l,t}$ and $O_{l,t}$ are new- and old-shell crab abundances in length-class l and year t , M_t is instantaneous natural mortality in year t , m_l is molting probability, $R_{l,t}$ is recruitment, y is lag between abundance assessment and the fishery, and $P_{l',l}$ is the proportion of molting crab growing from length l' to length l after one molt. $C_{l',t}$ is catch (legal males) or handling mortality (sublegal males and females). Recruitment is defined as recruitment to the model and survey gear rather than recruitment to the fishery. $P_{l',l}$ and $R_{l,t}$ are computed as follows.

Mean growth increment per molt is assumed to be a linear function:

$$(A2) \quad G_l = a + b\tau$$

where a and b are constants. Growth increment per molt is assumed to follow a gamma distribution:

$$(A3) \quad g(x|\alpha, \beta) = x^{\alpha-1} e^{-x/\beta} / (\beta^\alpha \Gamma(\alpha))$$

The expected proportion of molting individuals growing from length-class l_1 to length-class l_2 after one molt is equal to the sum of probabilities with length range (τ_1, τ_2) of the receiving length class l_2 at the beginning of next year, i.e.,

$$(A4) \quad P_{l_1, l_2} = \int_{\tau_1 - \tau}^{\tau_2 - \tau} g(x|\alpha, \beta) dx$$

where τ is the midlength of length-class l_1 .

Recruitment is separated into a time-dependent variable, R_t ,

and a length-dependent variable, U_l , representing the proportion of recruits belonging to each length-class:

$$(A5) \quad R_{l,t} = R_t U_l$$

where U_l is described by a gamma distribution similar to eqs. A3 and A4 with parameters α_r and β_r .

For each year, annual effective spawning biomass, SP_t , was estimated as

$$(A6) \quad SP_t = r_t \sum_l [F_{l,t} WF_l], \quad \tau \geq 90 \text{ mm CL}$$

where $F_{l,t}$ is female abundance in length-class l and year t , WF_l is mean weight of female crab in length-class l , τ is the midlength of length-class l , and r_t is the ratio of male reproductive potential MRP_t to total mature female abundance TMF_t (≥ 90 mm CL) in year t , i.e.,

$$(A7) \quad r_t = \begin{cases} MRP_t / TMF_t, & \text{if } MRP_t < TMF_t \\ 1, & \text{if } MRP_t \geq TMF_t \end{cases}$$

That is, if $r_t \geq 1$, then there are sufficient mature males to mate with all mature females, and so the number of spawning females is equal to the number of mature females. If $r_t < 1$, then not enough mature males are available to mate all mature females and the number of spawning females will be a fraction of mature females.

Male reproductive potential is defined as

$$(A8) \quad MRP_t = \sum_l [(N_{l,t} + O_{l,t}) mn_l], \quad \tau \geq 120 \text{ mm CL}$$

where $N_{l,t}$ and $O_{l,t}$ are mature male crab abundances in length-class l and year t with new- and old-shell conditions, respectively, and mn_l is the maximum number of females mated by a male in length-class l .

Annual recruitment is described by a general S-R model:

$$(A9) \quad R_t = SP_{t-k}^{r1} e^{r2 - r3 SP_{t-k} + v_t}$$

where k is recruitment age, $r1$, $r2$, and $r3$ are constants, and environmental noise $v_t = \delta_t + a1 v_{t-1}$. δ_t was assumed as a $N(0, \sigma)$.